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Alignment Ability of Strabismic and Eye Enucleated Subjects on the Horizontal and Oblique Meridians

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For normal sighted observers visual performance is often superior on the principal meridians than on the oblique. There has been no clear consensus on whether disruption of the visual system affects performance on orientation sensitivity tasks. Here we compare the abilities of normally sighted subjects tested monocularly, subjects with one eye enucleated and strabismic subjects using the non-deviating eye, in an orientation task. Subjects were asked to align a dot with a bar that was oriented either horizontally or on the oblique. For all groups, alignments were significantly more accurate and precise for the horizontal bar as compared to the oblique bar. Normally sighted subjects were significantly more precise on alignments in the horizontal and oblique planes than strabismic subjects, using the non-deviating eye. Precision for eye enucleated subjects was similar to that of normally sighted subjects. Precision of alignments did not correlate to the age at diagnosis of strabismus or to depth of amblyopia in strabismus. We conclude that for alignment ability, the disruption of visual development produced by enucleation of one eye is not equivalent to that produced by strabismus. This could represent an underlying difference in the visual system between these two groups.

Orientation sensitivity Strabismus Eye enucleation

INTRODUCTION

Visual performance for many observers, on visual tasks such as grating acuity, contrast sensitivity, vernier acuity and alignment tasks, is superior on the principal meridians than off axis (Essock, 1990; Gwiazda, Bauer, Thorn & Held, unpublished results; Regan & Maxner, 1986; Vogels, Orban & Vandenbussche, 1984). Although, as Vogels and Orban (1991) state, studies of orientation tuning are affected by many factors (e.g. attention, eye movements, anaesthesia), most researchers agree that meridional variations in visual performance are due to neural factors (see e.g. Ferster & Koch, 1987; Orban, Vanderbussche, Sprague & De Weerd, 1990; Vogels & Orban, 1990, 1991). As evidence, these anisotropies still exist even when the optics of the eye are bypassed (Campbell, Kulikowski & Levinson, 1966).

Orientation anisotropies have been demonstrated in human infants within the first 6 months of life (Gwiazda, Brill, Mohindra & Held, 1978; Leehey, Moskowitz-Cook, Brill & Held, 1975; Sokol, Moskowitz & Hansen, 1987; but see Teller, 1974). These studies indicate that anisotropies may occur without visual experience. Studies of individuals with abnormal visual experience, however, lead to mixed conclusions about the role of visual experience in anisotropies of orientation (see Gwiazda *et al.*, unpublished results; Levi, Harwerth & Smith, 1979; Mitchell, 1980; Mitchell, Freeman, Millodot & Haegerstrom, 1973; Rentschler & Hilz, 1979; Sireteanu & Singer, 1980; Vandenbussche, Vogels & Orban, 1986; Vogels *et al.*, 1984). Fregnac, Shulz, Thorpe and Bienenstock (1992) further showed that orientation preference could be changed in cats by driving cells iontophoretically while stimulating them with a non-preferred orientation. These preferences could be induced even outside the critical period, suggesting that visual experience may play a role in the development or maintenance of orientation preference.

One way to examine the role of visual experience on orientation preference is to study animals that have had vision interrupted artificially. Fregnac, Trotter, Bienenstock, Buisseret, Gary-Bobo and Imbert (1981) examined the developmental properties of neurons in V1 in

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normal and unilaterally enucleated cats. Fregnac *et al.* found that the removal of one eye at birth altered neuronal development in terms of orientation selectivity. In 6 week old eye enucleated kittens, there was an over representation of cells preferring horizontal and vertical orientations, as compared to normally reared kittens. These researchers concluded that binocular competition plays a vital role in the process of orientation selectivity. In contrast, Shook, Maffei and Chalupa (1985) found that cats that had one eye removed at least 2 weeks before birth, showed a full 180 deg cycle of preferred orientations and did not find over representation of the principal axes. Shook *et al.*, however, did report that they encountered receptive fields that were smaller than those found in control animals.

Clearly, if as Fregnac *et al.* (1981) suggest, binocular competition plays a vital role in the development of orientation selectivity, we would expect changes in the behavioural performance of eye enucleated human subjects. Following eye enucleation, the remaining eye would have complete competitive advantage (no competition). From Fregnac *et al.*'s study, it could be predicted that the remaining eye of the eye enucleated patient would show larger differences in performance between the horizontal and oblique conditions than would normally sighted observers, due to over representation of cells on the principal meridians in enucleated patients. However, from Shook's data, it could be predicted that there would be normal performance in the remaining eye and better precision due to smaller receptive fields.

It is likely that data based on eye enucleation cannot explain the behavioural performance of strabismic subjects. For many early onset strabismic subjects, much visual information to the strabismic eye is suppressed. There is, therefore, a competitive advantage given to the non-strabismic eye (assuming that the suppression occurs at or before the cite of binocular competition). Many physiological studies have shown that strabismus often results in a reduction of cortical binocularity (e.g. Hubel & Wiesel, 1965; von Noorden, 1990). However, suppression in strabismus is neither uniform nor complete (von Noorden, 1990) and the effects of this incomplete binocular competition may be evident in the strabismic subject. This weakened binocular competition and suppression might affect each subject's ability to align objects in different orientations. Further, the effect on orientation tasks of variables, such as the degree of amblyopia and age at onset of strabismus in strabismic subjects, must be clarified.

We have previously examined vernier acuity, optokinetic symmetry, egocentre location and monocular depth perception in subjects with varying levels of binocular competition (Gonzalez, Steinbach, Ono & Wolf, 1989; Gonzalez, Steinbach & Rush-Smith, 1992; Moidell, Steinbach & Ono, 1988; Reed, Steinbach, Anstis, Gallie, Smith & Kraft, 1991). In this paper we compare the ability of subjects, with varying levels of binocular competition, to align objects in horizontal and oblique orientations.

MATERIALS AND METHODS

Normal subjects

Thirty-four normally sighted children and adults ranging in age from 4.3 to 31.0 yr served as subjects. All subjects had near normal vision of 20/20 in each eye and performed normally on the Randot stereo test (Stereo Optical Co., Inc.).

Strabismic subjects

Twenty-six patients from the ophthalmology clinic at The Hospital for Sick Children in Toronto served as subjects. Age ranged from 4.2 to 31.0 yr. The age at which strabismus was diagnosed was between 3 and 171 months. Patients with alternating strabismus or nystagmus (including latent nystagmus) were excluded. Twenty patients showed constant esotropia while six patients showed constant exotropia (one consecutive exotropia, post surgery). Only the non-deviating eye of these patients was tested. In the eyes tested, refractive error (including spherical errors or spherical equivalents) ranged from -0.63 to $+4.75$ D. Eight subjects showed an astigmatism in the eye tested. In six of these subjects the axis of astigmatism was between 80 and 90 deg. Three of these six subjects showed a mild astigmatism (<0.75 D cylindrical), one showed a moderate astigmatism (2.25 D cylindrical) and two showed high astigmatism (4.25 and 7.25 D cylindrical). In one subject there was a very mild (0.25 D cylindrical) astigmatism at 150 deg, while the remaining subject showed a moderate (1.5 D cylindrical) astigmatism at 180 deg. All subjects were tested while wearing their refractive correction. Two subjects had visual acuities of 20/30 in the non-deviating eye, while in three others the acuity of this eye was 20/40. All the remaining subjects had acuities within normal limits in the eye tested. In the non-tested deviating eye visual acuities ranged from 20/20 to 20/200. The course of treatment varied greatly among patients.

Eye enucleated subjects

Twenty-one patients, who were monocularly enucleated and were being followed at The Hospital for Sick Children in Toronto, served as subjects. All had been enucleated because of unilateral retinoblastoma, except for one who had Coat's disease. In all subjects the remaining eye was ophthalmologically normal. Age at testing ranged from 5.0 to 18.3 yr. Age at eye enucleation ranged from 3 to 47 months. Acuities for these patients were within normal limits and refractive errors in these eyes ranged from -0.65 to $+1.88$ D (spherical errors or spherical equivalents). Four of these subjects showed astigmatism in the eye tested. All astigmatisms were at 90 deg and all were mild (<1 D cylindrical). All subjects were tested with full optical correction. Prior to eye enucleation eight subjects showed an eye deviation in the affected eye (five showed esotropia, three showed exotropia). In seven of these eight patients, the strabismus was first noted in medical records within 6 months of surgery (all but one subject was eye enucleated before 24 months), while in the remaining subject strabismus was noted at birth (eye enucleated at 18 months). However, the angle of strabismic deviation was not measured in any subject.

Apparatus and procedure

Subjects were tested at The Hospital for Sick Children. The subject sat one meter in front of the screen (18 × 14 cm) of a Macintosh Plus micro computer. Normally sighted subjects had the non-preferred eye patched and strabismic subjects had the strabismic eye patched. The apparatus and method was modelled after Salomon (1947), Bouma and Andriessen (1968, 1970) and a recent variation of the Salomon procedure by Pavel, Cunningham and Stone (1992). The stimulus was a black bar (2.9 deg length and 8.2 min, arc width), which was oriented at either 0 (horizontal) or 45 deg. Located 3.9 deg away (regardless of dot position) from the right hand tip of the bar was a dot (9.4 min arc diameter), which could be moved by key presses on the Macintosh keyboard. Each key press moved the centre to centre location of the dot 20 arc min. The dot moved in an arc pattern so that the distance between the dot and the right-hand tip of the bar remained at 3.9 deg. On the 40 consecutive trials, the start position of the dot varied randomly along the possible dot positions. On 20 trials, the bar was in the horizontal position and on 20 trials the bar was in the oblique position. These oblique and horizontal trials were randomly presented on consecutive trials. The subjects were required to align the dot with the bar. Children were motivated to align the dot and the bar, as the display was described as a shooting gallery. After the alignment the child could press a button which would make the dot, via an animation sequence, appear to explode. This alignment task was chosen over a pure test of orientation discrimination because it was simple for our young subjects to understand and the procedure was quick to perform. Since our subjects included children and all were patients being seen at The Hospital for Sick Children, it was important to minimize the time of the procedure to fit with the patient's appointment and with the attention span of the children. It was because of these time constraints that we chose only to run two stimulus orientations.

RESULTS

Both precision and average alignment of each subject's performance were measured. Precision was calculated as the SD of 20 responses each for the horizontal target and for the oblique target. Average alignment was calculated as the mean alignment response of the subject subtracted from perfect alignment.

As shown in Fig. 1, for every group (normal, enucleate and strabismic) subjects were more precise with the horizontal than the oblique target ($F_{1,78} = 208.82$, $P < 0.0001$). There was also a significant effect of the group tested ($F_{2,78} = 4.5$, $P < 0.05$). Strabismic subjects were found to be less precise in both the horizontal and the oblique conditions than were the normal subjects (Tukey Studentized Range > 3.379, $P < 0.05$). No significant differences in precision were found between the eye enucleated subjects and the strabismic subjects or between the eye enucleated subjects and the normal subjects. This suggests that as a group enucleate subjects do perform normally, however, some individual enucleate patients do show imprecision in the alignment task (as evidenced by group variability).

All subjects showed significant differences in average alignment (accuracy) between oblique and horizontal conditions, with the horizontal estimations being closer to perfect alignment than oblique ($F_{1,78} = 83.64$, $P < 0.0001$). This was unexpected because our task should only isolate differences in precision, not accuracy. The inaccurate oblique measures may have resulted from some asymmetry in the display, but a subsequent study showed this constant error occurred even when subjects viewed the target through a circular aperture (i.e. the horizontal edge of the computer screen was eliminated from view*). We speculate that there may be some Poggendorff-type illusion (see Day, 1989; Day & Stecher, 1993; Day, Stecher & Parker, 1993) causing the equal magnitude oblique misalignments across all groups ($F_{2,78} = 0.59$, $P > 0.05$).

There were no significant correlations between average alignment and the age of the subject in any subject group. Further, there were no significant correlations between average alignment and age at enucleation or strabismic onset, between average alignment and refractive error in the eye tested of strabismic or eye enucleated subjects and between average alignment and the degree of amblyopia in strabismic subjects. Also, there were no significant correlations between precision and age at enucleation or strabismic onset, between precision and

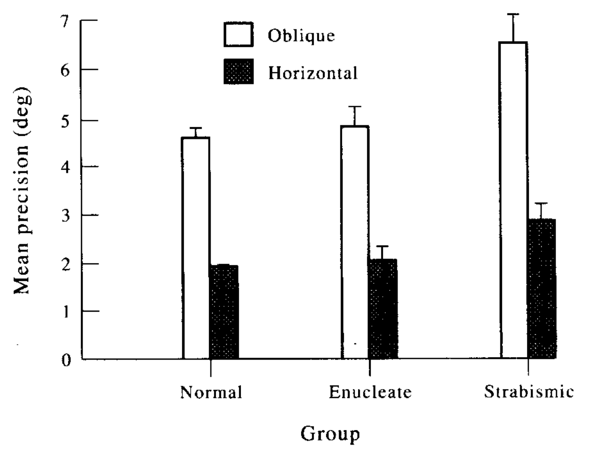

FIGURE 1. Mean precision and SE for normal, enucleate and strabismic subjects aligning in the oblique (white bar) and horizontal (shaded bar) orientations.

*To ensure that the differences in accuracy between the horizontal and oblique conditions could not be attributed to the borders of the rectangular computer screen, a control study was run. In this study, all methods and procedures remained the same except that these seven subjects viewed the display through a circular aperture that covered the rectangular borders of the screen. The results remained unchanged. The subjects were again significantly more accurate at making alignments in the horizontal direction than the oblique direction.

refractive error* in the eye tested of strabismic or eye enucleated subjects and between precision and the degree of amblyopia in strabismic subjects. Although there were no significant correlations between precision and visual acuity in the eye tested for eye enucleated subjects, there were small but significant correlations ($r < 0.40$) between precision and acuity in the eye tested for strabismic subjects. Such a small correlation can only account for less than 16% of the variation in these data. There were significant correlations between age at the time of testing and precision of alignment for all subject groups (Control, $r = -0.5$, -0.4; Enucleate, $r = -0.8$, -0.7; Strabismic, $r = -0.7$, -0.6, for oblique and horizontal alignments respectively). Older subjects tended to be more precise than younger subjects.

Since precision is related to the age of the subject, we wanted to ensure that our results were not due to age differences between strabismic and normal groups. From our samples we selected and analysed data from normal and strabismic subjects whose birth was within the strict criterion of 6 months. Average precision for the age selected strabismic subjects (6.6 deg oblique; 2.6 deg horizontal) and age selected normal subjects (4.5 deg oblqiue; 1.9 deg horizontal) was virtually the same as that reported in Fig. 1 and in the initial analysis. Statistically, these precision values between normal and strabismic subjects approached significance for this age selected sample ($F_{1,34} = 3.48$, $P < 0.07$). The reduction in significance from the analysis of data in Fig. 1 to this age controlled sample, was due to the reduction in the number of subjects that we were able to age match within 6 months.

DISCUSSION

Our study uncovered a number of interesting findings. First, all subjects (normal subjects monocularly tested, strabismic subjects using the non-deviating eye and eye enucleated subjects) showed that alignments on the horizontal meridian were both more precise and more accurate than alignments on the oblique meridian. This result was not unexpected and confirms earlier work (see e.g. Bouma & Andriessen, 1968, 1970). Second, eye enucleate subjects were similar to normal subjects in their accuracy and precision of alignments on both the horizontal and oblique axis. Finally, strabismic subjects using the non-deviating eye were similar to normal subjects and eye enucleate subjects in accuracy on both the horizontal and oblique axis, but strabismic subjects using the non-deviating eye were less precise than normal subjects in horizontal and oblique alignments.

We did not find, as Frenac's physiological data would imply, that eye enucleated subjects showed larger differences between horizontal and oblique alignments than normal subjects. We also did not find, as might be expected from the small receptive field size reported by Shook *et al.* (1985), that eye enucleated subjects were more precise in alignments than normals. Further, we did not find any correlation between age at enucleation and alignment ability in our eye enucleated subjects. Therefore, behavioural performance of human eye enucleated subjects is not accurately predicted from these animal studies. It is, however, possible that with different stimuli we could find differences between normal and eye enucleated subjects. Our stimulus had a minimum 20 min arc step size. If the differences between eye enucleated subjects and normal subjects are subtle, then our stimuli might not be sensitive enough to detect them. Further, some enucleate subjects do show less precision than do normal subjects as evidenced by the non-significant difference between strabismic and eye enucleate subjects in precision judgements.

The finding that, on average, the eye enucleated subjects performed normally is not entirely unexpected. Many studies show that enucleation (pre and post natal) in animals can substantially change the physiological development of the visual system at the level of the LGN and at the collicular level (Casagrande & Condo, 1988; Finlay, Sengelaub & Berian, 1986; Garraghty, Shatz Sretaban & Sur, 1988; Instausti, Blakemore & Cowan, 1985; Ostrach, Crabtree & Chow, 1986; Rakic, 1986; Reese, 1986; Shen & Baisden, 1986; Thurlow & Cooper, 1985). However, behavioural studies show eye enucleated humans to be unaffected in the remaining eye in terms of vernier acuity (Gonzalez *et al.*, 1992), optokinetic symmetry (Reed *et al.*, 1991) and use of parallax information in depth perception (Gonzalez *et al.*, 1989).

We did find that strabismic subjects, regardless of acuity, age at diagnosis and refractive status were less precise in both horizontal and oblique alignments than normally sighted subjects. Bedell, Flom and Barbeito (1985) had shown previously that for both eyes of amblyopic strabismic subjects, there was imprecision in aligning a vertically oriented target. Here we find that strabismic subjects were imprecise when using their non-affected eye for alignment tasks involving the horizontal and oblique axis. This might suggest that the visual system of the strabismic subject differs from normally sighed subjects. Alignment tasks might highlight a "noisy" visual system. The idea of a "noisy" visual system has recently been explored by Hess and Field (1994), Levi, Klein and Wang (1994a, b) and Levi, Waugh and Beard (1994c). This neural noise might be exhibited as imprecision.

We found, as did Bedell *et al.*, that strabismic subjects show similar to normal accuracy (average alignment) in target alignments. The fact that all subject groups perform similarly on average alignment estimates in both

*To ensure that imprecision in the strabismic group was not due to astigmatism, the precision of strabismic subjects who showed astigmatism were directly compared to precision values for strabismic subjects who showed no astigmatism. No statistical differences in precision values on either the horizontal or the oblique conditions were found between astigmatic strabismic subjects and non-astigmatic strabismic subjects. We also examined the precision of the four enucleate subjects who showed mild astigmatism. These subjects showed no consistent pattern of precision. One subject showed less precision than the enucleate group, one showed more precision than the enucleate group while the other two had precision values close to the mean of the enucleate group.

oblique and horizontal conditions, may be in part due to the methodology rather than similarities between groups. Any distortion in the subject's visual system would exist for both the bar and the dot. Thus an alignment task between the bar and dot would not reveal the distortion. It is therefore not surprising that all subject groups in this study and in Bedell *et al.*'s study showed similar average alignments between groups.

There have been many hypotheses to explain the improved visual performance on tasks involving the horizontal meridian over tasks involving the oblique meridian (see e.g. Appelle, 1972; Emmerson, Wenderoth, Curthays & Edmonds, 1975; Vogels & Orban, 1991; Wenderoth, Beh & White, 1978). Suggested explanations include both environmental and physiological causes. This study cannot resolve the issue of cause. Regardless of the cause, we find that all our groups (normal, eye enucleated and strabismic) show marked improvement in accuracy and precision of alignment on the horizontal axis over the oblique axis. Strabismic subjects, however, show less precision on both the horizontal and oblique axis than do normal and eye enucleated subjects.

Visual development is affected by both competitive and non-competitive mechanisms (Sherman & Spear, 1982). Competition can be examined by comparing behavioural visual development in patients who have experienced either early monocular or early binocular form deprivation. Presumably, in monocular deprivation, the non-deprived eye has competitive advantage, while there is no obvious advantage for either eye in binocular deprivation. Such studies have revealed that binocular competition is involved in the development of visual acuity and contrast sensitivity (Maurer, Lewis & Brent, 1989). We speculate that competitive mechanisms could be involved in the development of the precision of alignment. The strabismic subject would have partial competition between the eyes, since suppression in the deviating eye of the strabismic is almost always regional (von Noorden, 1990). The normally sighted subject would have complete binocular competition between the eyes, while the eye enucleated subject would have little to no competition (some competition could have occurred before eye enucleation). We suggest that binocular competition at the level present in strabismus is more disruptive to precision of alignments than those levels present in eye enucleation (little to no competition) and in normally sighted subjects (complete competition). Jampolsky (1978) also found that the severity of early visual deficits increases when combined with strabismus. We do recognize that some other factor unique to strabismus, such as increased neural noise, might be causing imprecise alignments to occur.

One of the hazards of studying patient populations is the uncontrollable heterogeneity. Among other things, strabismic patients differ in the type and the severity of the deviation, the age at onset of the deviation, the age at diagnosis of the strabismic condition and the treatment. Enucleates vary in the degree of vision present, the size of the tumor, intraocular pressures, etc. Any study of these "noisy" populations must make allowances for the intrinsic variability among patients. We did examine a number of these variations and to date could not find any that were correlated to our main effects.

Our results do show that the disruption of visual development produced by enucleation is not equivalent to that produced by strabismus. Whether this represents an underlying difference in the visual system of these two groups or that strabismic deficits are more severe because of remaining competitive mechanisms is yet to be determined.

REFERENCES

Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: The "oblique Effect" in man and animals. *Psychological Bulletin, 78,* 266–278.

Bedell, H. E., Flom, M. C. & Barbeito, R. (1985). Spatial aberrations and acuity in strabismus and amblyopia. *Investigative Ophthalmology and Visual Science, 26,* 909–916.

Bouma, H. & Andriessen, J. J. (1968). Perceived orientation of isolated line segments. *Vision Research, 8,* 493–505.

Bouma, H. & Andriessen, J. J. (1970). Induced changes in the perceived orientation of line segments. *Vision Research, 10,* 333–348.

Campbell, F. W., Kulikowski, J. J. & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. *Journal of Physiology, London, 187,* 427–436.

Casagrande, V. A. & Condo, G. J. (1988). Is binocular competition essential for layer formation in the lateral geniculate nucleus? *Brain, Behavior and Evolution, 31,* 198–208.

Day, R. H. (1989). Natural and artificial cues, perceptual compromise and the basis of veridical and illusory perception. In Vickers, D. & Smith, P. L. (Eds), *Human information processing: measures, mechanisms and models.* London: Elsevier.

Day, R. H. & Stecher, E. J. (1992). Some variant forms of the Poggendorff Illusion and their implications for an explanation. *Bulletin of the Psychonomic Society, 30,* 26–28.

Day, R. H., Stecher, E. J. & Parker, A. L. (1993). The effect of edge orientation and movement direction on the apparent misalignment of collinear bars. *Perception & Psychophysics, 53,* 642–647.

Emmerson, P., Wenderoth, P., Curthoys, I. & Edmonds, I. (1975). Measuring perceived orientation. *Vision Research, 15,* 1031–1033.

Essock, E. A. (1990). The influence of stimulus length on the oblique effect of contrast sensitivity. *Vision Research, 30,* 1243–1246.

Ferster, D. & Koch, C. (1987). Neuronal connections underlying orientation selectivity in cat visual cortex. *Trends in Neuroscience, 10,* 487–492.

Finlay, B. L., Sengelaub, D. R. & Berian, C. A. (1986). Control of cell number in the developing visual system. 1. Effects of monocular enucleation. *Developmental Brain Research, 28,* 1–10.

Fregnac,Y., Shulz, D., Thorpe, S. & Bienenstock, E. (1992). Cellular analogs of visual cortical epigenesis. 1. Plasticity of orientation selectivity. *Journal of Neuroscience, 12,* 1280–1300.

Fregnac, Y., Trotter, Y., Bienenstock, E., Buisseret, P., Gary-Bobo, E. & Imbert, M. (1981). Effect of neonatal unilateral enucleation on the development of orientation selectivity in the primary visual cortex of normally and dark-reared kittens. *Experimental Brain Research, 42,* 453–466.

Garraghty, P. E., Shatz, C. J., Sretavan, K. W. & Sur, M. (1988). Axon arbors of X and Y retinal ganglion cells are differentially affected by prenatal disruption of binocular inputs. *Proceedings of the National Academy of Science, U.S.A., 85,* 7361–7365.

Gonzalez, E., Steinbach, M. J., Ono, H. & Rush-Smith, N. (1992). Vernier acuity in monocular and binocular children. *Clinical Vision Science, 7,* 257–261.

Gonzalez, E., Steinbach, M. J., Ono, H. & Wolf, M. (1989). Depth perception in humans enucleated at a early age. *Clinical Vision Sciences, 4,* 172–177.

Gwiazda, J., Brill, S., Mohindra, I. & Held, R. (1978). Infant visual acuity and its meridional variation. *Vision Research, 18,* 1557–1564.

Hess, R. F. & Field, D. J. (1994). Is the spatial deficit in strabismic amblyopia due to loss of cells or an uncalibrated disarray of cells. *Vision Research, 34,* 3397–3406.

Hubel, D. H. & Wiesel, T. N. (1965). Binocular interaction in striate cortex of kittens reared with artificial squint. *Journal of Neurophysiology, 28,* 1041–1059.

Insausti, R., Blakemore, C. & Cowan, W. M. (1985). Postnatal development of the ipsilateral retinocollicular projection and the effects of unilateral enucleation in the golden hamster. *Journal of Comparative Neurology, 234,* 393–409.

Jampolsky, A. (1978). Equal visual inputs and strabismus management: A comparison of human and animal strabismus. *Transactions of the New Orleans Academy of Ophthalmology* (pp. 358–492). St Louis, MO: Mosby.

Leehey, S. C., Moskowitz-Cook, A., Brill, S. & Held, R. (1975). Orientation anisotropy in infant vision. *Science, 190,* 900–902.

Levi, D. M., Harwerth, R. S. & Smith, E. L. (1979). Humans deprived of normal binocular vision have binocular interactions tuned to size and orientation. *Science, 206,* 852–854.

Levi, D. M., Klein, S. A. & Wang, H. (1994a). Amblyopic and peripheral vernier acuity: A test-pedestal approach. *Vision Research, 34,* 3265–3292.

Levi, D. M., Klein, S. A. & Wang, H. (1994b). Discrimination of position and contrast in amblyopic and peripheral vision. *Vision Research, 34,* 3293–3313.

Levi, D. M., Waugh, S. J. & Beard, B. L. (1994c). Spatial scale shifts in amblyopia. *Vision Research, 34,* 3315–3333.

Maurer, D., Lewis, T. L. & Brent, H. P. (1989). The effects of deprivation on human visual development: Studies of children treated for cataracts. In Morrison, F. J., Lord, C. & Keating, D. P. (Eds), *Applied developmental psychology, Vol. 3, psychological development in infancy* (pp. 39–227). San Diego, Calif.: Academic Press.

Mitchell, D. E. (1980). The influence of early visual experience on visual perception. In Harris, C. S. (Ed.), *Visual coding and adaptability* (pp. 1–50). Hillsdale N.J.: Erlbaum.

Mitchell, D. E., Freeman, R. D., Milloot, M. & Haegerstrom, G. (1973). Meridional amblyopia: Evidence for the modification of the human visual system by early visual experience. *Vision Research, 13,* 535–558.

Moidell, B., Steinbach, M. J. & Ono, H. (1988). Egocenter location in children enucleated at an early age. *Investigative Ophthalmology and Visual Science, 29,* 1348–1351.

von Noorden, G. K. (1990). *Binocular vision and ocular motility. Theory and management of strabismus.* Toronto: Mosby.

Orban, G. A., Vanderbussche, E., Sprague, J. M. & De Weerd, P. (1990). Orientation discrimination in the cat: A distributed function. *Proceedings of the National Academy of Science, U.S.A., 87,* 1134–1138.

Ostrach, L. H., Crabtree, J. W. & Chow, K. L. (1986). The ipsilateral retinocollicular projection in the rabbit: An autoradiographic study of postnatal development and effects of unilateral enucleation. *Journal of Comparative Neurology, 254,* 369–381.

Pavel, M., Cunningham, H. & Stone, V. (1992). Extrapolation of linear motion. *Vision Research, 32,* 2177–2186.

Rakic, P. (1986). Mechanism of ocular dominance segregation in the lateral geniculate nucleus: Competitive elimination hypothesis. *Trends in Neurosciences, 9,* 11–15.

Reed, M. J., Steinbach, M. J., Anstis, S. M., Gallie, B., Smith, D. & Kraft, S. (1991). The development of optokinetic nystagmus in strabismic and monocularly enucleated subjects. *Behavioural Brain Research, 46,* 31–42.

Reese, B. E. (1986). The topography of expanded uncrossed retinal projections following neonatal enucleation of one eye: Differing effects in dorsal lateral geniculate nucleus and superior colliculus. *Journal of Comparative Neurology, 250,* 8–32.

Regan, D. & Maxner, C. (1986). Orientation-dependent loss of contrast sensitivity for pattern and flicker in multiple sclerosis. *Clinical Vision Sciences, 1,* 1–23.

Rentschler, I. & Hilz, R. (1979). Abnormal orientation selectivity in both eyes of strabismic amblyopes. *Experimental Brain Research, 37,* 187–191.

Salomon, A. D. (1947). Visual field factors in the perception of direction. *American Journal of Psychology, 60,* 68–88.

Shen, C. L. & Baisden, R. H. (1986). Expansion of the ipsilateral retinal projection to the medial terminal nucleus of the accessory optic system in rats with one eye removed. *Experimental Neurology, 93,* 270–274.

Sherman, S. M. & Spear, P. D. (1982). Organization of visual pathways in normal and visually deprived cats. *Physiological Reviews, 62,* 738–855.

Shook, B. L., Maffei, L. & Chalupa, L. M. (1985). Functional organization of the cat's visual cortex after prenatal interruption of binocular interactions. *Proceedings of the National Academy of Science, U.S.A., 82,* 3901–3905.

Sireteanu, R. & Singer, W. (1980). The "vertical effect" in human squint amblyopia. *Experimental Brain Research, 40,* 354–357.

Sokol, S., Moskowitz, A. & Hansen, V. (1987). Electrophysiological evidence for the oblique effect in human infants. *Investigative Ophthalmology and Visual Science, 28,* 731–735.

Teller, D. Y. (1974). Visual acuity for vertical and diagonal gratings in human infants. *Vision Research, 14,* 1433–1439.

Thurlow, G. A. & Cooper, R. M. (1985). Increased dependence of superior colliculus metabolic activity on visual cortex after eye enucleation. *Experimental Neurology, 90,* 594–600.

Vanderbussche, E., Vogels, R. & Orban, G. A. (1986). Human orientation discrimination: Changes with eccentricity in normal and amblyopic vision. *Investigative Ophthalmology and Visual Science, 27,* 237–245.

Vogels, R. & Orban, G. A. (1990). How well do response changes of striate neurons signal differences in orientation: A study in the discriminating monkey. *Journal of Neuroscience, 10,* 3543–3558.

Vogels, R. & Orban, G. A. (1991). Quantitative study of striate single unit responses in monkeys performing and orientation discrimination task. *Experimental Brain Research, 84,* 1–11.

Vogels, R. Orban, G. A. & Vandenbussche, E. (1984). Meridional variations in orientation discrimination in normal and amblyopic vision. *Investigative Ophthalmology and Visual Science, 25,* 720–728.

Wenderoth, P., Beh, H. & White, D. (1978). Perceptual distortion of an oblique line in the presence of an abutting vertical line. *Vision Research, 18,* 923–938.

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